

2 **Ecological limitations to the resilience of coral reefs**

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6 **Abstract** The decline of coral reefs has been broadly
7 attributed to human stressors being too strong and perva-
8 sive, whereas biological processes that may render coral
9 reefs fragile have been sparsely considered. Here we
10 review several ecological factors that can limit the ability
11 of coral reefs to withstand disturbance. These include: (1)
12 Many species lack the adaptive capacity to cope with the
13 unprecedented disturbances they currently face; (2) human
14 disturbances impact vulnerable life history stages, reducing
15 reproductive output and the supply of recruits essential for
16 recovery; (3) reefs can be vulnerable to the loss of few
17 species, as niche specialization or temporal and spatial
18 segregation makes each species unique (i.e., narrow eco-
19 logical redundancy); in addition, many foundation species
20 have similar sensitivity to disturbances, suggesting that
21 entire functions can be lost to single disturbances; and (4)
22 feedback loops and extinction vortices may stabilize
23 degraded states or accelerate collapses even if stressors are
24 removed. This review suggests that the degradation of coral
25 reefs is due to not only the severity of human stressors but
26 also the “fragility” of coral reefs. As such, appropriate

governance is essential to manage stressors while being
inclusive of ecological process and human uses across
transnational scales. This is a considerable but necessary
upgrade in current management if the integrity, and
delivery of goods and services, of coral reefs is to be
preserved. **33**

Keywords Diversity · Ecosystem function · Biodiversity
loss · Conservation · Stability · Coral reef ecology **35**

Introduction **36**

Coral reefs constitute one of the most diverse, socioeco-
nominically important and threatened ecosystems in the
world (Wilkinson 2002; Bellwood et al. 2004; Burke et al.
2011). Coral reefs harbor thousands of species (Reaka-
Kudla 1997; Fisher et al. 2015) and provide food and
livelihoods for millions of people, while safeguarding
coastal populations from extreme weather disturbances
(Wilkinson 2002; Adger et al. 2005; Burke et al. 2011).
Unfortunately, the world’s coral reefs are rapidly degrading
(Wilkinson 2002; Bellwood et al. 2004; Burke et al. 2011),
with ~19% of the total coral reef area effectively lost
(Wilkinson 2002) and 60–75% under direct human pres-
sures (Wilkinson 2002; Burke et al. 2011; Mora 2015).
While some coral reefs have shown the capacity to recover
from major disturbances (Gilmour et al. 2013; Graham
et al. 2015), the majority of reefs are displaying a general
decline in live coral cover (Gardner et al. 2003; Bruno and
Selig 2007; De’ath et al. 2012), and some have moved to
“non-coral” states, for example, dominated by macroalgae
or, at times, bivalves, sponges, tunicates, zoanths, or
octocorals (Hughes 1994; Wilkinson 2002; Mumby et al.
2006; Bruno et al. 2009; Dudgeon et al. 2010; Graham 58

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59 et al. 2015). The economic and ecological value of coral
60 reefs makes understanding the causes of their decline
61 imperative.

62 The decline of coral reefs has been broadly attributed to
63 threats emerging from climate change and widespread
64 human expansion in coastal areas, which has facilitated
65 exploitation of local resources, assisted colonization by
66 invasive species, and led to the loss and degradation of
67 habitats through fishing and runoff from agriculture and
68 sewage systems (Wilkinson 2002; Gardner et al. 2003;
69 Hughes et al. 2003; Pandolfi et al. 2003; Bellwood et al.
70 2004; Bruno and Selig 2007; Norström et al. 2009; Dud-
71 geon et al. 2010; Burke et al. 2011; De'ath et al. 2012;
72 Erfteimeijer et al. 2012; Graham et al. 2015). These dis-
73 turbances vary from global (e.g., warming, acidification) to
74 local but occurring over vast geographical areas (e.g.,
75 fishing, pollution) (Knowlton 2001; Mora 2008; Mora et al.
76 2011), vary in their effects from antagonistic to additive to
77 synergistic (Knowlton 2001; Darling and Côté 2008; Dar-
78 ling et al. 2010), from having direct to indirect effects over
79 species (Hughes et al. 2003; Bellwood et al. 2004; Côté and
80 Darling 2010), and some can be chronic and slow, but may
81 interact with pulse and fast disturbances increasing sus-
82 ceptibility to community shifts (Nyström et al. 2000).

83 The magnitude of human stressors is an obvious and
84 commonly cited reason for the decline of coral reefs. This
85 decline, however, could be compounded by the less com-
86 monly and sparsely considered limits of ecological resi-
87 lience in coral reefs. Here we undertake a review of these
88 factors and show that coral reefs have several ecological
89 "weaknesses" to disturbances. The reduced ecological
90 resilience of coral reefs combined with the severe and
91 widespread distribution of stressors imposed by human
92 activities raises considerable concerns for the long-term
93 viability of coral reefs and the goods and services they
94 provide while highlighting the urgent need for effective
95 governance. Although at times we have drawn ecological
96 knowledge from other marine ecosystems, our review is
97 not intended to provide a contrast of the resilience of coral
98 reefs to other ecosystems.

99 Limited adaptability

100 **AQ1** It is possible that the relative historical stability of tropical
101 environments inhabited by coral reefs has led organisms
102 and ecosystems poorly adapted to environmental change
103 (McClanahan et al. 2002). Consequently, contemporary
104 human activities that change the intensity and spatial
105 coverage of certain environmental variables (e.g., warm-
106 ing, acidification) and/or introduce novel stressors (e.g.,
107 new species, fishing, pesticides, cyanide, heavy metals) can
108 have profound impacts on coral reefs. Indeed physiological

109 studies have revealed that many coral species have toler-
110 ances to temperature and pH very close to ambient tem-
111 perature and pH (Hoegh-Guldberg et al. 2007; Hoegh-
112 Guldberg and Bruno 2010), although considerable varia-
113 tion exists among species and geographic locations in
114 bleaching susceptibility (Pandolfi et al. 2011; Palumbi et al.
115 2014). Another well-known example of low resistance to
116 human pressures is that of mega-fauna extinction due to
117 exploitation (e.g., dugongs, sharks; Jackson 1997; Jackson
118 et al. 2001; Pandolfi et al. 2003; Ward-Paige et al. 2010).
119 These species typically experience limited natural mortal-
120 ity and thus have evolved life histories of slow growth and
121 late sexual maturity that make them highly vulnerable and
122 prone to extinction due to even mild levels of human
123 exploitation (Jackson 1997; Jackson et al. 2001; Pandolfi
124 et al. 2003; Ward-Paige et al. 2010).

125 Many species on coral reefs appear to lack adaptations
126 to withstand recent extreme and unprecedented stressors.
127 Available data for vertebrate species suggest that rates of
128 adaptation to cope with projected climate change over the
129 next 100 yr would need to be >10,000 times faster than
130 rates typically observed (Quintero and Wiens 2013),
131 although some evidence suggests that acclimatization and
132 adaptation to thermal stress (Palumbi et al. 2014), and
133 ocean acidification (McCulloch et al. 2012) can occur
134 fairly quickly in some species of corals and reef fishes
135 (Donelson et al. 2012; Miller et al. 2012). The capacity for
136 acclimation and adaptation among species is currently
137 poorly known, because much of this research is in its
138 infancy and restricted to a handful of species. However, the
139 observed declines of coral reefs so far indicate that coral
140 reefs have and will modify their compositions and func-
141 tioning based on the survivors of modern threats (Pandolfi
142 et al. 2011; Graham et al. 2014).

Impaired meta-populations

143
144 Most species on coral reefs, including fishes and inverte-
145 brates, have a bipartite life cycle, with a dispersive pelagic
146 larval stage and a highly sedentary, benthic adult phase.
147 These life history characteristics mean that the persistence,
148 and hence functional roles, of most species on coral reefs
149 inherently depends on meta-population dynamics (i.e.,
150 patches of habitats occupied by adults that are connected
151 by larval dispersal). Unfortunately, coral reef meta-popu-
152 lations are highly vulnerable to human stressors.

Meta-population connectivity

153
154 Connectivity is an integral part of resilience in the face of
155 chronic or stochastic disturbances, because it can maintain
156 functions over broader scales and act as a store for

157 replenishment, genetic supply, and adaptability potential
 158 (Nyström and Folke 2001; Nyström et al. 2008; Halford
 159 and Caley 2009). The interaction among human stressors
 160 on coral reefs can pose several double jeopardies to the
 161 dispersal and replenishment of reef fish population. For
 162 instance, habitat loss can increase isolation among reef
 163 patches, whereas warming can accelerate larval develop-
 164 ment and settlement (Bergenijs et al. 2005; Levin 2006);
 165 as a result, larvae will have larger distances to travel but
 166 shorter times to do so (Munday et al. 2009; Hoegh-Guld-
 167 berg and Bruno 2010; Mora and Sale 2011; Figueiredo
 168 et al. 2014). Likewise, chronic local human stressors (e.g.,
 169 fishing, pollution) could shift the structure of local
 170 assemblages toward long-distance dispersers (given high
 171 mortality of self-recruiting species: Bellwood et al. 2004).
 172 This could also be detrimental to recruitment because long-
 173 distance dispersers may face poor growing conditions
 174 (Swearer et al. 1999) and thus may face higher mortality
 175 upon recruitment (Bergenijs et al. 2002). Pollutants can
 176 also prevent larvae from detecting settlement cues (Markey
 177 et al. 2007; Wenger et al. 2015) and can act as a barrier to
 178 larval recruitment (Richmond 1993).

179 **Meta-population patches**

180 Local adult populations in meta-population patches are
 181 fundamental to the supply of the propagules necessary for
 182 recovery, but are the prime direct and indirect targets of
 183 human activities. Coastal pollution (e.g., oil, heavy metals,
 184 pesticides), for instance, can interfere with chemical sig-
 185 nals in corals, leading to impaired reproductive synchrony
 186 among coral colonies (Peters et al. 1997), possibly result-
 187 ing in an Allee effect despite a high density of colonies.
 188 Likewise, fishing directly removes individuals from local
 189 populations (Roberts 1995) preventing fish of reaching
 190 larger sizes and of producing more eggs (eggs are produced
 191 in proportion to a fish's volume, which is proportional to
 192 the cube of its length; Lubchenco et al. 2003; Palumbi
 193 2004). Eggs from larger or older mothers can also be of
 194 better quality and thus have higher chances of survival
 195 (Lubchenco et al. 2003; Palumbi 2004). Experimental
 196 studies have also demonstrated that intense fishing can
 197 reduce fish body size (Conover and Munch 2002) and lead
 198 to maladaptive strategies such as producing smaller and
 199 fewer eggs (Conover and Munch 2002; Walsh et al. 2006;
 200 Conover et al. 2009). Likewise, the ongoing loss (Gardner
 201 et al. 2003; Bruno and Selig 2007) and homogenization of
 202 coral reefs (Pratchett et al. 2008; Alvarez-Filip et al. 2009;
 203 Rogers et al. 2014) can lead to the intensification of eco-
 204 logical interactions, such as predation and competition and
 205 thus a reduction in local populations and reproductive
 206 output (Pratchett et al. 2008; Forrester and Steele 2013;
 207 Rogers et al. 2014). This can occur for at least two reasons:

(1) As reefs become architecturally simpler, they provide 208
 fewer refuges from predation (Pratchett et al. 2008; For- 209
 rester and Steele 2013), and (2) because simpler reefs 210
 increase encounters among competitors, thus increasing 211
 their exposure to predators (Hixon and Beets 1993; Hixon 212
 and Carr 1997; Pratchett et al. 2008). The diminishing 213
 complexity and supply of refuges in the context of eco- 214
 logical interactions suggests that reef populations will 215
 experience density-dependent mortality, even as popula- 216
 tions get smaller (Hixon and Beets 1993; Hixon and Carr 217
 1997; Loreau 2004; Forrester and Steele 2013). 218

Limited insurance in diverse systems

In diverse ecosystems, numerous species are expected to 220
 have similar functional roles ("redundancy"), different 221
 tolerances to one ("response diversity") or several ("co- 222
 tolerance") disturbances, such that the functional role of a 223
 lost species can be replaced by those that endure the dis- 224
 turbance (Nyström 2006; Nash et al. 2014). However, 225
 evidence for coral reefs often contrasts to those expected 226
 responses. 227

Limited functional redundancy

It is intuitive to imagine that in a large pool of species, 229
 there will be numerous species with similar ecological 230
 functions (Bellwood et al. 2004). On coral reefs, the idea of 231
 functional redundancy is supported by the fact that the 232
 number of functional groups saturates as the number of 233
 species increases; in other words, there are many more 234
 species than functional groups, indicating that multiple 235
 species play similar functional roles: They are redundant 236
 (Halpern and Floeter 2008; Mora et al. 2011). However, a 237
 saturating relationship between richness and functional 238
 diversity is not fully indicative of functional redundancy, as 239
 it fails to indicate the frequency of species within func- 240
 tional groups. For instance, exploration of the frequency 241
 distribution of species within functional groups has 242
 revealed strong right-skewed frequencies, with few func- 243
 tional groups having lots of species or large abundances, 244
 and most functional groups having a handful and at times 245
 single species or few individuals (Bellwood et al. 2004; 246
 Mouillot et al. 2013; Stuart-Smith et al. 2013). In the 247
 Caribbean, for instance, much of the historical rugosity of 248
 coral reefs was provided by *Acropora cervicornis* and *A.* 249
palmata (Pandolfi and Jackson 2006), which have almost 250
 completely disappeared due to considerable damage by 251
 extreme hurricanes and disease outbreaks (Nyström et al. 252
 2000). Likewise, the functional role of bioerosion on Indo- 253
 Pacific reefs is largely played by the giant humphead par- 254
 rotfish (*Bolbometopon muricatum*), which is highly 255

256 vulnerable to fishing due to its large size and life history
257 (Bellwood et al. 2003). Even rare species have been known
258 to lack functional analogs for performing key functions in
259 coral reef ecosystems (Mouillot et al. 2013).

260 The idea that diverse coral reefs have large redundancy
261 within functional groups may also be ill-conceived,
262 because of the gross classifications of functional groups.
263 For instance, deeper exploration of morphological (Price
264 et al. 2011) and dietary (Burkepile and Hay 2008) char-
265 acteristics of species generally classified as herbivorous
266 have revealed the existence of considerable differences
267 among species. Such differences may result from niche
268 specialization and have non-trivial effects on resilience.
269 For instance, variations in the palatability of algae (Littler
270 et al. 1983) suggest that a broad portfolio of “herbivores”
271 are required to keep algae in check (i.e., functional com-
272 plementarity within a functional group; Burkepile and Hay
273 2008; Rasher et al. 2013) and that resilience could be
274 highly dependent on a few species that specialize in the
275 consumption of unpalatable algae (e.g., Bellwood et al.
276 2006a; Johansson et al. 2013). This suggests that it is not
277 the total diversity that matters for resilience, but how
278 diversity is apportioned across different functional groups.

279 The assumption that coral reefs have high ecological
280 redundancy can also be misleading by the strong focus on
281 single traits/characteristics. For example, a diverse assem-
282 blage characterized solely on the feeding behaviors of the
283 constituent species may give a sense of high ecological
284 redundancy because many species are likely to be part of
285 the same feeding groups. However, when species are fur-
286 ther considered in the context of their home range, pre-
287 ferred feeding times and substrate, bite rates, and
288 reproductive rates, the notion of high species redundancy is
289 reduced (Peterson et al. 1998; Isbell et al. 2011). Petchey
290 and Gaston (2007) demonstrated that the levels of func-
291 tional redundancy decrease if many functional dimensions
292 are used, and increases if fewer dimensions are used.
293 Likewise, some species classified as generalists based on
294 their diet can be very specialized with regard to foraging
295 grounds (Brandl et al. 2015); the loss of such species may
296 have critical effects on feeding functions in certain areas of
297 reefs. Clearly, redundancy may not be as extensive in coral
298 reefs as one would expect from their high diversity
299 (Micheli and Halpern 2005; Stuart-Smith et al. 2013),
300 suggesting that entire functions and, by default, ecosystem
301 functioning can be vulnerable to the loss of a handful of
302 species (see also Jain et al. 2014). Functional redundancy
303 in ecological systems has also been questioned from a
304 theoretical perspective because this should drive species to
305 extinction mediated by competition (Loreau 2004); in other
306 words, functional redundancy implies that species share
307 many similar habits, which can trigger competition and a
308 reduction in species fitness.

309 If ecological specialization is pervasive in coral reefs,
310 it will imply that the ecological roles of many species can
311 be unique to the functioning of coral reefs and that
312 ecosystem functioning should increase exponentially with
313 the addition of new species because resource use opti-
314 mization rather than loss due to competitive interactions is
315 likely to prevail (Mora et al. 2014). Indeed, Mora et al.
316 (2011) found that standing biomass (used as proxy for
317 functioning) increased exponentially with the addition of
318 new species, indicating the unique contributions of spe-
319 cies to ecosystem functioning. They also found that given
320 similar levels of disturbance, standing biomass was sig-
321 nificantly reduced in more diverse ecosystems, further
322 highlighting the lack of redundancy and high vulnerability
323 of diverse coral reef ecosystems. The large spatial varia-
324 tions in species richness across geographical regions
325 suggest that levels of ecological redundancy can vary
326 greatly among places, which may help to explain
327 observed spatial variations in the resilience of coral reefs
328 to similar human stressors (Bellwood et al. 2004; Roff and
329 Mumby 2012).

330 Our argument above is that the specialization that has
331 been commonly argued to allow for the coexistence of
332 many species in coral reefs (Sale 1977, 1980; Wainwright
333 and Bellwood 2002) can lead to reductions in functional
334 redundancy. It should be acknowledged, however, that
335 specialized morphological adaptations in other diverse
336 ecosystems have not necessarily resulted in specialized
337 habits (the so-called Liem’s paradox; Liem 1980). The
338 flexibility to exploit resources beyond those to which
339 species have specialized adaptations is possible if the
340 specialized phenotype is still efficient in processing other
341 resources, especially when preferred resources are low. In
342 coral reef fishes, there is a broad evidence of niche parti-
343 tioning along food (Robertson et al. 1979; Robertson and
344 Gaines 1986) and habitat (Robertson and Gaines 1986;
345 Brandl and Bellwood 2014) resources, as well as consid-
346 erable declines in abundance when specific habitat (Mun-
347 day 2004; Pratchett et al. 2012) and food items (Pratchett
348 et al. 2008) have declined, suggesting that specialization
349 does exist among some reef fishes. However, there is also
350 evidence that specialized phenotypes do not necessarily
351 have specialized diets, supporting Liem’s paradox (Bell-
352 wood et al. 2006b). Further studies showed, however, that
353 while species with specialized morphological adaptations
354 may have generalized diets, they may have subtle parti-
355 tioning of feeding microhabitats cautioning the use of
356 morphological adaptations to assess specialization (Brandl
357 et al. 2015). This is not to say that there are not ecological
358 roles that can be played by many species, but that the
359 functioning of coral reefs is vulnerable to the loss of few
360 species with specialized functions (Brandl and Bellwood
361 2014).

362 **Limited response diversity and negative co-tolerance**

Inherent in the idea that biodiversity confers resilience is that similar functional species will have differential sensitivity to stressors to ensure ecosystem recovery by the more resistant species within a given functional group (Elmqvist et al. 2003). However, high diversity may offer limited resilience if all species within a functional group respond equally to the same stressor, which may be common on coral reefs (Nyström et al. 2000; Bellwood et al. 2004; Nyström et al. 2008). Fishing, for instance, can impose a similar detrimental impact over many species of larger predators and large herbivores on coral reefs (Roberts 1995; Nyström et al. 2000; Bellwood et al. 2004; Micheli and Halpern 2005; Mora 2008; Mora et al. 2011). Similarly, branching and plating corals (e.g., Caribbean acroporids; Nyström et al. 2000), which provide most of the complexity of coral reefs, show comparable sensitivity to extreme hurricanes, warming, and disease outbreaks (Nyström et al. 2000; Darling et al. 2013; Rogers et al. 2014).

Resilience to co-occurring stressors should be maximized by biodiversity if adaptation to one stressor increases resistance to, or the number of species expected to survive, other stressors (i.e., positive co-tolerance) (Vinebrooke et al. 2004). For coral reefs, Darling et al. (2013) found limited evidence of positive co-tolerance. Fishing and bleaching events have filtered (i.e., selected against) different sets of coral species, although some species were equally susceptible to both stressors, leading to reefs dominated by few coral species (“survivors”) that are stress tolerant (i.e., typically slow growing massive species) or have opportunistic, weedy life histories that allow fast colonization. For reef fishes, Graham et al. (2011) showed that while fishing often targets large fishes, warming (via its effect on habitat loss) exerts greater effects on small-bodied and more coral-specialized species, resulting in the fish community being greatly reduced when both stressors co-occur. Failing to gain resilience to one stressor after facing another stressor is a considerable concern for the stability of coral reefs worldwide, given the overlapping extent and variety of human disturbances (Fig. 1).

404 **Feedback loops and extinction vortices**

Resilience in coral reefs could be further compromised by numerous ecosystem, demographic and genetic feedback loops, operating independently of local diversity that can stabilize degraded ecosystems or even accelerate the rate of decline (i.e., extinction vortices), even if stressors are removed.

Stabilizing ecosystem feedbacks

Several ecological processes can reinforce degraded ecosystem states (Hughes et al. 2010; Nyström et al. 2012; Shephard et al. 2012; Fung et al. 2013). For instance, a considerable loss of live coral cover (e.g., following hurricanes, coral bleaching episodes, disease) opens up space, and if conditions are right, opportunistic fast-growing algae can reach an abundance beyond the grazing capacity of the standing stock of herbivores (Williams et al. 2001; Mumby et al. 2007a). Increasing algal abundance can enhance coral mortality and prevent coral recruitment and survival (Mumby et al. 2007b), directly by reducing suitable substratum for settlement, causing shadowing, overgrowing, causing chemically driven allopathic exclusions (Nyström et al. 2012), or indirectly by enhancing microbial communities and diseases (Smith et al. 2006). Some herbivorous fish species avoid patches of high algal density (Hoey and Bellwood 2011), further aggravating the challenge of maintaining cropped macroalgae (Williams et al. 2001). A similar stabilizing mechanism has been suggested for fish communities facing intense exploitation (Shephard et al. 2012; Fung et al. 2013). That is, juveniles of large fishes can face excessive competition and predation by more abundant smaller species whose abundances are “relaxed” from competition and/or predation due to the loss of larger fishes (Fung et al. 2013). In the longer term, the loss of corals can reduce structural complexity, potentially reducing the populations of herbivores (Graham et al. 2006). Stabilizing feedback loops suggest that reversal of an ecosystem shift can be significantly impeded even after a stressor has been completely removed (Nyström et al. 2012; Shephard et al. 2012).

Extinction vortices due to demographic feedback loops

Extinction vortices can be triggered by demographic processes if low abundance results in individuals failing to find mates, leading to a reproduction shortfall as part of a process variously known as depensation, the Allee effect, and inverse density dependence (Myers et al. 1995; Gascoigne and Lipcius 2004). For instance, in large broadcasting corals, which contribute substantially to reef structure, fertilization can drop considerably just 3 h after the peak of spawning, suggesting that isolated colonies may fail to mix gametes, increasing the risk of recruitment failure (Oliver and Babcock 1992). Allee effects at reproduction, combined with heavy exploitation, may have been responsible for the extinction of giant clams (*Tridacna gigas*) from Fiji, Guam, New Caledonia and the Northern Marianas (Wells 1997). Deleterious effects of small population size on species also facing extensive exploitation should be more pronounced among sedentary species like

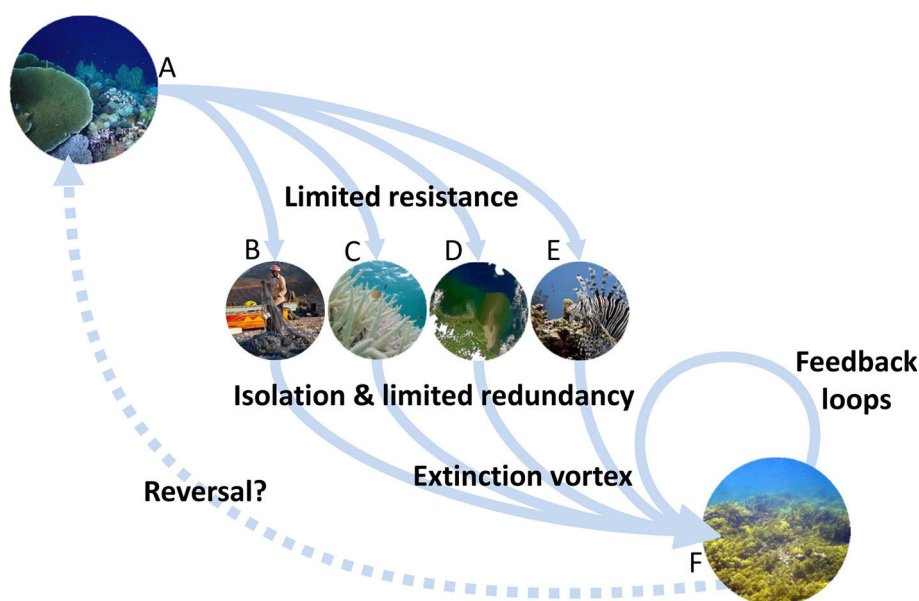


Fig. 1 General process of coral reef modification. Coral reefs are typified by high biological diversity and habitat complexity, largely provided by reef building corals (A). However, due to a plethora of anthropogenic stressors, such as fishing (B), climate change (C), nutrient and sediment inputs (D), and introduced species (E), many reefs around the world are in decline, and some have shifted to a new

ecosystem state, such as the one dominated by macroalgae (F). These shifts can become permanent due to several stabilizing feedback loops and even accelerate to more degraded systems by extinctions vortices. Photograph credits: A and F, Nick Graham; E, Emily Darling; B and C, Wikimedia Commons; D, MODIS Aqua satellite image, NASA OceanColor Web site (oceancolor.gsfc.nasa.gov/)

461 *Tridacna* (Wells 1997) or species that already occur in low
462 densities, such as sharks (Ward-Paige et al. 2010). Human
463 impacts may also reverse naturally occurring Allee effects
464 with detrimental effects on coral reef resilience. For
465 instance, populations of the coral-eating crown-of-thorns
466 starfish (*Acanthaster planci*) are thought to be naturally
467 low due to Allee effects (Dulvy et al. 2004). However,
468 fishing of starfish predators (Dulvy et al. 2004), in com-
469 bination with greater nutrient loads that greatly increase
470 growth and survival of starfish larvae (Brodie et al. 2005),
471 has been implicated in preventing Allee effects and may
472 cause outbreaks of the crown-of-thorns, which in turn
473 cause considerable reductions in live coral cover.

474 **Extinction vortices due to genetic loss** 475 **and “maladaptations”**

476 If populations are reduced considerably, genetic variation
477 may be reduced, which can completely truncate (Swain
478 et al. 2007) or significantly delay (Allendorf and Hard
479 2009) recovery, even if stressors are removed. This occurs
480 because genes are lost through adaptation by means of
481 anthropogenic selection and can be hard if not impossible
482 to replace (Swain et al. 2007). Reduced genetic diversity
483 can also decrease populations’ adaptive potential to natural
484 environmental variability, leading to higher genetic drift, or
485 the random loss of important alleles, and cause inbreeding
486 depression or increasing expression of recessive deleterious

genes and overdominant genes (Soulé and Mills 1998; 487
Tanaka 1998; Amos and Balmford 2001). 488

If population declines are caused by selective stressors, 489
this could lead to directional selection and “maladaptations” 490
that impair demographic processes and potentially 491
cause extinction in what has been defined as “evolutionary 492
suicide” (Rankin and Lopez-Sepulcre 2005). Evidence of 493
such “maladaptations,” or changes in life history traits 494
induced by human stressors, is diverse. For example, size- 495
selective fishing can induce substantial declines in fish 496
mean body size, fecundity, larval viability, and sex ratios, 497
which in turn detrimentally affect recruitment, yield, and 498
biomass (Walsh et al. 2006). Likewise, increasing warming 499
has been related to reductions in body size, clutch size, and 500
accelerated early development in several marine organisms 501
(reviewed by Hoegh-Guldberg and Bruno 2010). Although 502
the extent to which such “maladaptations” occur in nature 503
is largely unknown, this is likely to change as new 504
advances in genome-wide scanning improve our under- 505
standing of the genetic responses of organisms to anthro- 506
pogenic stressors. 507

508 **Paving a future for coral reefs**

Evidence of the decline of coral reefs worldwide is rela- 509
tively well documented (Wilkinson 2002; Gardner et al. 510
2003; Bellwood et al. 2004; Bruno and Selig 2007; 511

512 Paddock et al. 2009). While there are obvious stressors to
513 coral reefs (e.g., fishing, coastal pollution, climate change,
514 invasive species, diseases), our review shows that there are
515 also many ecological mechanisms that considerably limit
516 the capacity of coral reefs to cope with such stressors.
517 Coral reefs currently face a dangerous situation by being
518 “fragile” while dealing with stressors that are not only
519 intense but spatially pervasive (Nyström et al. 2000). There
520 is also evidence to suggest that the more degraded a coral
521 reef is, the harder it is to reverse the degradation. For
522 instance, Mumby et al. (2007a) modeled how reversing
523 coral–algae phase shifts through the restoration of herbiv-
524 orous fishes would require a fourfold increase in herbivores
525 at coral cover of ~5%, but only a twofold to threefold
526 increase at a coral cover of ~30%.

527 Having ecosystems that are fragile poses a major chal-
528 lenge for conservation because it suggests that the intensity
529 of disturbances has to be reduced considerably. This calls
530 for governance initiatives that are regional in scope and
531 integral in their assessment of stressors and ecosystem
532 limits while balancing human uses. These strategies should
533 better account for drivers of change (e.g., climate change,
534 migration, fishing, trade), ecosystem processes (e.g., dis-
535 persal and connectivity), policies (e.g., fisheries manage-
536 ment), and actors (e.g., fishers, coastal developers) and
537 should transgress borders of individual nations. The Coral
538 Triangle Initiative on Coral Reefs, Fisheries and Food
539 Security (CTI) is an example of one such attempt. The
540 intergovernmental agreement covers six nations (Indone-
541 sia, Malaysia, the Philippines, Timor Leste, Papua New
542 Guinea, and the Solomon Islands) with a mission to govern
543 common resources and strategically coordinate marine-
544 protected areas and climate adaptation actions (Fidelman
545 et al. 2012). Strengthening similar stewardship over larger
546 scales will be necessary for coral reefs to maintain their
547 integrity and to continue delivering the many goods and
548 services we obtain from them.
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